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Title: Global assessment of the effects of terrestrial acidification on plant species richness

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This is an earlier version of the following article: Azevedo LB, van Zelm R, Hendriks AJ, Bobbink R, Huijbregts MAJ (2013) Global assessment of the effects of terrestrial acidification on plant species richness. Environmental Pollution 174, 10-15.
<http://dx.doi.org/10.1016/j.envpol.2012.11.001>

ABSTRACT

This study estimates the potential losses of vascular plant species richness due to terrestrial acidification for different world's biomes. We used empirical occurrence data of 2409 species from 140 studies and estimated the relative species richness – pH response curves using logistic regressions. The regressions were then used to quantify the fraction of species that are potentially lost due to soil pH changes. Although we found considerable variability within biomes, our results show that the pH at which species richness was maximized was found to be the lowest in (sub)tropical forests (pH = 4.1) and the highest in deserts (pH = 7.4). We also found that (sub)tropical moist forests are highly sensitive to decreases of in soil pH below 4.1. This study can be coupled with existing atmospheric deposition models to quantify the risk of species richness loss following soil acidification.

Capsule: Relationships of potential species richness loss along a soil pH gradient are proposed

Graphical abstract

Keywords: terrestrial acidification, pH, species richness, species sensitivity distribution

INTRODUCTION

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Original sentence: Species richness and soil acidity relationships in biomes

Terrestrial acidification is a global threat to plant diversity and is mainly caused by atmospheric deposition of acidifying compounds (Dentener et al., 2006a). Soils of low pH or with low acid neutralizing capacity are generally characterized by increased mobilization and toxicity of aluminum and other metals, leaching of base cations, and decreased nitrification and organic matter decomposition rates (Bobbink et al., 2010; Knoepp and Swank, 1994; Matson et al., 1999).

As a result of changes in nutrient regulation, plants may suffer from a decrease in phosphorus and magnesium content in tissue, an increase in tissue yellowing, a reduction in biomass, coverage, and root growth, unsuccessful germination and regeneration, and competitive exclusion by acid-tolerant species (Falkengren-Grerup, 1986; Roem and Berendse, 2000; Zvereva et al., 2008). Consequently, decreased occurrence of plants in unsuitable, acidified soils has been reported in areas subjected to soil pH reductions in the past (Falkengren-Grerup, 1986; Roem and Berendse, 2000).

Here we focus on soil pH as an indicator of soil acidity since it is an important predictor of plant occurrence and it is correlated to many soil nutrients, e.g. base cations, and acidifying pollutants, e.g. aluminum and sulfur (Kozlov and Zvereva, 2011; Peppler-Lisbach and Kleyer, 2009; van Zelm et al., 2007).

Up to now, studies that relate soil pH with species richness have included only a limited number of ecosystems, most of which are in mid to high latitudes (Chytrý et al.,

2010; Olsson et al., 2009). Recently, climate has been shown to be an important predictor of the sensitivity of vascular plants to various pollutants (Kozlov and Zvereva, 2011). In warmer climates, for example, higher temperatures may increase the mobility of toxicants and the year-round production of tissue may enhance sensitivity to pollutants (Zvereva et al., 2008). In addition, larger plants or plants consisting of woody tissue appear to be more sensitive to acidifying pollution than small, soft tissue ones (Zvereva et al., 2010; Zvereva et al., 2008). To identify large regions according to their climate and ecological interactions and similarities (Orians, 1993), this study categorized the world into terrestrial biomes delineated by Olson *et al.* (2001). Classification on a biome level highlights the influence of soil pH while accounting for main climatic differences such as temperature, precipitation, or sunlight.

The objective of our paper is to develop response relationships of vascular species richness along the pH gradient for different world's biomes. The response relationships were attained for the acidic pH gradient, up to levels where vascular species richness is maximized. Here we define species richness as the total number of vascular species (trees, herbs, shrubs, etc) occurring on a soil of a given soil pH. Vascular plants are important not only because they comprise a vast number of species of plants but also due to their contribution to a considerable portion of primary production in the terrestrial system. Response relationships of species richness and pH can be used for predictions of the potential reductions of biodiversity due to soil

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property changes (van Zelm et al., 2007). Connecting pH response curves to pollutant transport models, including their impacts on soil properties, may give insight into the impact of acidifying pollution at large spatial scales, help identify sensitive areas, and indicate where acidifying pollution reduction efforts should be concentrated (Mac Nally and Fleishman, 2004; van Zelm et al., 2007).

MATERIAL AND METHODS

In order to estimate the relative vascular plant species richness – pH patterns, we first gathered field observational data from the literature relating individual species occurrence and soil pH to derive empirical relationships of species richness along the soil pH gradient. Second, we performed a logistic regression analysis to arrive at pH – response functions for the different biomes. The steps of gathering literature data to finally determining response functions are described below and illustrated in appendix 1 of the Supporting Information.

Data gathering

We collected peer-reviewed studies available up to September 2010 consulting Web of Science with the following keywords: (1) pH; and (2) either soil, ground, land, or terrestrial; and (3) either cover, abundance, species richness, species frequency, extinction, presence, absence, diversity, biodiversity, community, occurrence, or biomass; and (4) either plantation, plant, plants, vegetation, vegetative, flora, forest,

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tree, or trees. This keyword combination allowed the retrieval of approximately 4000 peer-reviewed studies that were considered for our data inventory. We then manually selected the studies that fulfilled the following criteria.

We excluded croplands or urban studies as they do not reflect the natural vegetation of the area and included studies based on abandoned, restored, re-vegetated areas, and semi-natural grasslands since they are also subjected to biodiversity losses due to terrestrial acidification. Additionally, we only included exploratory, survey studies that reported a specific quantitative relationship between pH and vascular plant species. We only considered species and not higher taxonomic groups (e.g. family, class, etc). An exception was made for genus-level records when those did not accompany any other species belonging to that genus. Lower taxonomic level records (i.e. subspecies, variety) were also included and were considered equal to a species record.

Data handling

First, pH values were standardized to a representative soil depth and to water extracted pH (pH-H₂O). When more than one pH was reported for a given soil (e.g. multiple horizons), we used the value that was closest to either the B horizon or to 50cm of soil depth. This is the soil horizon where there is accumulation of clay minerals such as iron and aluminum and the approximate depth at which roots are

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present in all biomes (Canadell et al., 1996). For the studies reporting soil pH by KCl or CaCl₂ and not by H₂O extraction (fifteen in total), we converted pH – KCl and pH – CaCl₂ values to pH-H₂O using data from the ISRIC-World Soil Information database (Batjes, 2009), appendix 2.

Second, we standardized the species name records using The Plant List (2010) so as to correct for synonyms. Since species occurrence was reported in different ways (i.e. biomass, percent cover, abundance) we adapted the data to a presence or absence format by transforming any number higher than zero to species presence and any zero value to species absence.

Subsequently, we allocated each of the selected studies to one of the biomes based on the vegetation coverage described by their authors. Studies describing a vegetation pattern that either did not fit the biome classification system described by Olson et al. (2001) or that were described as a transition zone between two biomes were excluded.

Following this, we derived the pH range at which each plant species can occur within the biome. We considered a species to be absent at pH values outside its reported pH range. The soil pH range obtained from each study was set equal to the mean pH \pm 1.645 times the reported standard deviation (i.e. 90% of sample population) following Latour et al. (1994). For forty studies that did not report mean and standard

deviation values, but the minimum – maximum pH ranges were used instead, e.g. Karim and Mallik (2008). Finally, we determined the range between the minimum and maximum pH of each specific plant species per biome as the pH occurrence range for that species. If a species was reported in more than one study within the same biome, we used the lower and upper pH boundaries as the overall species occurrence range. From the pH occurrence ranges of the species within each biome, we excluded the species that were reported at a single mean pH value (273 of 3311 species – biome combinations) because these data are not representative of the tolerance pH range where a species is found in the environment.

Response curves

We computed the species richness (S) as the sum of present species at each 0.1 pH unit i value within each biome j as

$$S_{i,j} = \sum_{pH_{i,j}} O_{i,j} \quad (1)$$

where O is the occurrence of each species at pH i in biome j . O is 0 when the species was reported absent and 1 if the species was reported present.

In a subsequent step, so as to compare biomes with dissimilar species richness, e.g. temperate vs. (sub)tropical forest, the species richness results in each biome were transformed into a zero-to-one measure described as the empirical potentially not

occurring fraction (ePNOF, equation 1) of species following Struijs et al. (2011) as

$$ePNOF_{i,j} = 1 - \frac{S_{i,j}}{S_{opt,j}} \quad (2)$$

where $S_{i,j}$ is the number of species present at pH i and $S_{opt,j}$ is the highest species richness along the pH gradient of biome j . An ePNOF of zero represents the optimum pH condition (pH_{opt}) or optimum pH conditions (range of pH_{opt}), where species richness equals $S_{opt,j}$; while an ePNOF of one represents the complete absence of species.

We calculated logistic functions of PNOF (cPNOF) by fitting them to the empirical ePNOF data. The use of logistic functions follows the calculation procedure commonly adopted in ecotoxicology to arrive at species sensitivity distributions for toxic chemicals and population modeling studies (De Zwart, 2001). They are represented as

$$cPNOF_{i,j} = \frac{1}{1 + e^{\frac{pH_{i,j} - pH_{opt,j}}{\beta_j}}}, \text{ for } pH_{i,j} \leq pH_{opt,j} \quad (3)$$

or

$$cPNOF_{opt,j} = 0, \text{ for } pH_{i,j} = pH_{opt,j} \quad (4)$$

where $cPNOF_{i,j}$ is the calculated PNOF at pH i of biome j below pH_{opt} (equation 3) or

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at the optimum pH (equation 4). At pH levels above pH_{opt} , species richness is not affected by acidic soil conditions but by other stressors, which we do not account in this study, such as sodium toxicity, etc. Coefficient α represents the pH at which 50 % of plant species potentially do not occur and β represents the relative change in species richness with pH. Biomes with low β values comprise the ecosystems with the steepest slope in the logistic function. We fitted the α and β coefficients using logistic regression in SAS 9.2. The sample size for cPNOF is given by the number of cPNOF – pH datapoints (with a 0.1 pH interval) observed from the lower end of the pH gradient up until the pH optimum. The confidence intervals were reported at a 95% confidence level.

Sensitivity analysis

In order to evaluate the uncertainty in the pH-response curves within biomes, we performed a sensitivity analysis for two additional levels of spatial aggregation: Ecoregion and individual sites (study) within each biome. That was attained by allocating the studies to ecoregions instead of biomes (Olson et al., 2001). Ecoregions are biogeographical subunits of specific biomes thus they offer a higher resolution of the existing vegetation. We then used the same methodology as described above and derived ecoregion-specific and site-specific logistic functions.

RESULTS

A total of 140 studies fulfilled our selection criteria (appendix 3) which, in total, comprised 2409 vascular plant species (see appendix 4 for their respective pH range within each biome). The number of studies within biomes varied from 2 (i.e. flooded grasslands and savanna, mangrove, and montane grassland and shrubland) to 55 (temperate broadleaf mixed forest), table 1. The location of each study is shown in figure 1.

Figure 1

Table 1

Table 2

In (sub)tropical moist broadleaf forests, the optimum pH was the lowest (4.1) while in desert and xeric shrublands and mediterranean forests, woodland and scrub, the optimum pH was the highest (7.4 to 7.8). Biomes within the temperate zone have rather similar optimum pHs, i.e. broadleaf mixed and coniferous forests, and grassland, savanna, and shrubland (4.7 to 5.1). The logistic regressions for all biomes indicate an association between increasing PNOF and pH decreasing (Figure 2).

Figure 2

Our results show that (sub)tropical moist broadleaf forest have steep cPNOF slopes ($\beta = 0.18$ to 0.25 , Table 2). This indicates that terrestrial acidification could

cause the highest increases in PNOF (thus the steepest species loss) in that biome.

Studies were available for a total of fifty-six ecoregions distributed across the thirteen biomes for comparisons of different spatial aggregation levels, (Table 1, appendix 5) and we were able to derive logistic functions for nineteen of them (Table 2, appendix 5). At a site (i.e. study) spatial resolution, we were able to derive logistic functions for thirty-three out of 140 individual studies (Table 3, appendix 5). We found higher optimum pHs for ecoregions (from 7.0 to 7.5) and sites (from 7.0 to 8.3) within desert and xeric shrubland compared to temperate broadleaf mixed forest and (sub)tropical moist broadleaf forests, which varied from 4.0 to 7.2 at the ecoregion level and 4.0 to 7.5 at the site level. Likewise, α values were consistently higher in desert and xeric shrublands (from 6.2 to 8.3) compared to temperate broadleaf mixed forest and (sub)tropical moist broadleaf forest (from 3.1 to 6.1). However, no difference was observed in β results across biomes at the ecoregion and site spatial resolution level.

DISCUSSION

We predicted the relative vascular plant species richness – soil pH patterns, expressed as the potentially not occurring fraction (PNOF) of species aggregated at the ecosystem (biome) level. In the following, we discuss the sources of uncertainty involved in our study. Furthermore, we assess the validity of our results by suggesting

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ecological arguments for the differences in the PNOF – pH relationships across ecosystems.

Uncertainty

First, it should be stressed that the PNOF reveals relative changes in overall vascular plants richness but not in individual species. Also, we do not analyze differentiated responses of specific functional traits, of specific native plants, or taxonomic groups. Hence, designating an optimum (or range of optimum) pH based on the maximized number of species may not necessarily associate with the most least modified, most “pristine” soil condition. Our results should thus be interpreted at the community level instead of at the species level.

Secondly, the number of studies differed considerably across biomes, which affected the number of species available in each biome (Table 1). For example, despite the high biodiversity in (sub)tropical biomes, we found more species reported in the temperate broadleaf mixed forest biome (Table 1). Given the low number of species available to derive logistic regressions in poorly covered biomes (e.g. mangroves, mediterranean forest, woodland, and scrub, and flooded grassland and savanna), the results for these biomes should be interpreted with caution. Therefore, interpretation is focused on biomes which are better covered by a number of studies and species.

Thirdly, for the temperate broadleaf mixed forest biome especially, there were a

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Original term: grassland, savanna, and shrubland

large number of European studies found. Given that we clustered all the studies into the same biogeographical region, there may be an over-representation of European species in this biome.

A fourth source of uncertainty is that our regressions were based on empirical data reporting the occurrence of plant species at a particular pH range. Our assumption is that, outside that range, the species was not observed thus it may have become absent, i.e. potentially not occurring. Within the pH occurrence range, the species is always considered to be present. Ultimately, in our field-based study, species absence could have been due to an unreported species occurrence outside the pH boundaries. Our approach differs from controlled, laboratory-based standard species sensitivity distributions, where the environmental conditions and the species of interest are deliberately chosen (Posthuma et al., 2002; Tilman, 1987). In controlled studies, conditions that determine species presence can be ascertained with a higher level of certainty. If the ranges of species occurrence were broader than what we were able to

determine, the species richness would be maintained at lower pH conditions.

Accordingly, the pH level where PNOF is 0.5 would be lower than those currently reported.

Fifth, the conversion of pH-KCl and pH-CaCl₂ to pH-H₂O could have introduced uncertainty to the range of pH occurrence of each species. The conversion from CaCl₂ and KCl to H₂O extracted pH varied up to 1 and 2 pH units, respectively

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Removed sentence since it is equal to second sentence of this paragraph: As a consequence, in our field-based study, species absence could have been due to an unreported species occurrence outside the pH boundaries.

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(appendix 2). This uncertainty may have been larger in temperate grassland, savanna, and shrubland and temperate broadleaf mixed forest biomes, where 17 to 20% of studies required conversion. Desert and xeric shrublands required no conversion to H₂O-extraction.

Our data set encompasses present-time, exploratory species occurrence studies of the last 20 years. Since acidifying pollution began much earlier than this, we cannot account for potential adaptation strategies that plants may have developed prior to the modification of the environment, e.g. increase in β -diversity, even though such adaptations are known to exist (Kozlov and Zvereva, 2011; Trubina and Vorobeichik, 2012). Also, a biome located in an area that has been exposed to intense air pollution, e.g. temperate broadleaf mixed forests, may have species that are less representative of their original assemblage or may have optimum pH lower than prior to air pollution compared to biomes which were subjected to acid deposition. Availability of nutrients such as nitrogen and phosphorus, which also relates to soil pH, may explain part of the remaining co-variance (Roem and Berendse, 2000).

Finally, the log-logistic results at the ecoregion and site spatial resolutions showed that there can be major differences between the logistic regression results representing plant communities of a biome. This may be remedied by applying more spatial to derive the regressions. However, this approach would include considerably fewer species per spatial unit and a reduced range of pH where species occur.

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Original term: considerable less

Consequently, the logistic regression we proposed often did not fit the empirical data at an increasing level of spatial resolution. This inherent spatial variability may also be explained by the existence of ecoregions transitioning between two ecosystems, e.g. the Central forest-grassland transition ecoregion, or of studies corresponding to a certain biome but that are located within the boundaries of another biome (open circles in Figure 1). In these cases, the studies were allocated to biomes based on their vegetation description, not their position in the map.

Response curves

The differences in the pH optima and the response curves across biomes may be explained by intrinsic differences across biomes. Soil pH follows a latitudinal gradient in which the highest pH values occur at mid latitudes (approximately 30° distant from the Equator line) while the lowest pH values occur in tropical regions (Pärtel, 2002). This trend is similar for the optimum pH of biomes found in this study (Fig. 2 in appendix 2). For example, the highest optimum pH is observed in soils of deserts and xeric shrublands, which are subjected to low precipitation and cation accumulation combined with high soil evaporation (Smith et al., 2002). Intermediately, mid to high latitude biomes, located in the temperate zone, are subjected to continuous sediment deposition from glaciations, e.g. temperate grassland, savanna, and shrubland (Pärtel, 2002). Conversely, (sub)tropical moist forests, generally comprising “ancient” soils, have low soil pH because they are subjected to strong long-term weathering of base

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cations without additional input of nutrient-rich sediments, in addition to increased solubility of ammonium, aluminum and manganese (Matson et al., 1999).

The adaptation of plants to specific environmental conditions for which they have been subjected is explained by the species pool hypothesis (Hajek et al., 2007; Pärtel, 2002). Species richness is maximized at low pH values in traditionally low soil pH biomes and at high pH values in traditionally high soil pH biomes (Chytrý et al., 2010; Pärtel, 2002). For example, in southwestern African desert, the highest number of species was found between pH levels of 7.0 to 7.5 (Medinski et al., 2010) while in the Appalachian Mountains, comprising temperate broadleaf mixed forests, maximum species richness is found at a pH of 4.0 to 5.0 (Peet et al., 2003). The high tolerance to acidic conditions in (sub)tropical moist broadleaf forests is also reflected by the high incidence of species belonging to families that are known to comprise a large number of aluminum-tolerant plants, i.e. Melastomataceae, Theaceae, and Symplocaceae (Hayde Gonzalez-Santana et al., 2012).

Species richness – soil pH relationships are often reported as linear (Schuster and Diekmann, 2003). However, even though the fraction of species that potentially disappear increases with decreasing pH, this rate is reduced at increasingly acidic conditions, suggesting that the species richness – pH relationship is non-linear. While species that cannot sustain acidic conditions are reduced, the total number of species is still maintained by a few ‘specialist’ species that are able to sustain (or exist

exclusively) at acidic conditions or that are able to adapt to new conditions, such as grasses (Falkengren-Grerup, 1986; Kozlov and Zvereva, 2011).

Although we found that (sub)tropical moist forests hold the highest number of species at acidic conditions, they are also highly sensitive to further increases in acidity compared to other biomes. This is illustrated by the steeper slope (lower β coefficient) of the log-logistic function, which represents the change in sensitivity associated with variation in soil pH.

Two aspects (the size and the physiology of plants) may help to explain the difference in the sensitivity of biomes to acidifying conditions. Previous studies report that grasses and smaller plants (herbaceous) are less sensitive to pollutants (e.g. aluminum or SO₂) than larger plants (Zvereva et al., 2010; Zvereva et al., 2008). Broadleaf mixed forests and grassland, savanna, and shrublands in the temperate zone were comprised of a high number of grasses and sedges (species of the Cyperaceae, Juncaceae, and Poaceae families). Small size plants, which are adapted to lessen evapotranspiration, dominated the desert and xeric shrubland biome, e.g. species of the Amaranthaceae and Cactaceae families. (Sub)tropical moist forests, on the other hand, encompassed large evergreen trees, e.g. Lauraceae, Myrtaceae species.

Toxic levels triggered by acidic conditions are particularly harmful to young roots (Zvereva et al., 2008). In addition, roots tend to grow to deeper layers in arid soils

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Original sentence: Previous studies report that grasses and smaller size plants (herbaceous) are less sensitive to pollution than larger size plants (Zvereva et al., 2010; Zvereva et al., 2008).

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Original sentence: the vertical distribution of roots in arid soils tends to be more concentrated in deeper layers

(Wilcox et al., 2004), which may become less exposed to the deposition of acidifying compounds. In opposition to colder (higher latitude) biomes, the high rate and year-round production of plant tissue in (sub)tropical moist forests may increase tissue exposure to acidic conditions and increase their sensitivity to low pH conditions. Mangroves, likewise, may be exposed to heavy metals following oxygenation of iron sulfide-rich soils (Amaral et al., 2011). The decreasing sensitivity to pollution with increasing latitude and decreasing temperature and precipitation has been observed in previous meta-analysis studies (Zvereva et al., 2010; Zvereva et al., 2008).

Conclusion

The results of this study describe general patterns that illustrate the increase in the fraction of species that may disappear with acidifying conditions at a spatial resolution equivalent to biomes. When a sensitivity analysis at higher spatial resolutions was performed (ecoregions and individual sites), we identified a considerable spatial variability within biomes, especially in the slope (β) of the logistic regressions, β . Furthermore, the results relating to many biomes were based on a small number of available species due to the low availability of studies performed in these regions. In this study, we used biomes as the spatial resolution since enhancing geographical coverage can increase the explanatory power of biogeographical patterns such as species richness – pH relationships (Field et al., 2009).

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Our results suggest that regions within the (sub)tropical moist broadleaf forest may suffer great changes in species richness following a soil acidification. This is an alarming situation given that soils in the (sub)tropical climate zone have very low acid neutralizing capacity (Dentener et al., 2006b; Kuylensstierna et al., 2001). The results of our study can be used with atmospheric pollutant transport and soil fate models so as to link acidifying air emissions to their ultimate biodiversity risk.

ACKNOWLEDGEMENTS

This research was funded by the European Commission under the 7th framework program on environment; ENV.2009.3.3.2.1: LC-IMPACT – Improved Life Cycle Impact Assessment methods (LCIA) for better sustainability assessment of technologies, grant agreement number 243827. We thank the three reviewers for comments on the previous version of the manuscript, Pierre-Olivier Roy for his advice on data compilation, Joop J.H. Schaminée for his advice on plant taxonomy, Rob S. E. W. Leuven for methodological insights, and Jon Matthews for proofreading the text.

SUPPLEMENTARY MATERIAL

Appendix 1: Description of the methodological steps taken in our study

Appendix 2: Conversion coefficients from (a) pH-KCl to pH-H₂O and from (b) pH-CaCl₂ to pH-H₂O and typical pH values per biome.

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Original term: soils in the (sub)tropical climate zone encompass soils

377 **Appendix 3:** List of studies in each biome, the number of species and the pH range of
378 each study.

379 **Appendix 4:** List of pH occurrence per species per biome

380 **Appendix 5:** Sensitivity analysis of the variability within biomes

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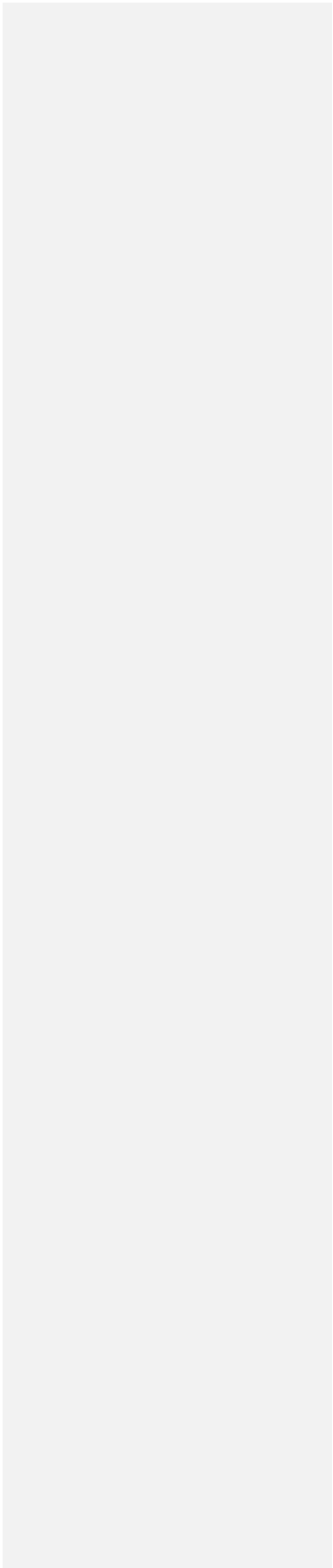
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507



509 **Table 1**

510 Total number of studies and species per biome, the total number of species in the
511 optimum pH, the pH range of species occurrence and the (range of) optimum pH.

512

513 **Table 2**

514 The optimum pH and the logistic regressions coefficients α and β (95% confidence
515 interval) for PNOF curves

516

Figure 1

Biomes delineated by Olson et al. (2001) and the location of the 142 sites included in our study. The sites where the described vegetation in each study corresponds to the biome where it is located (total of 113) and where the described vegetation is outside the boundaries of the corresponding biome (total of 29) are represented by closed and open circles, respectively.

Figure 2

Examples of response curves for the potentially not occurring fraction (PNOF) of plant species along the soil pH range shown for **(a)** (sub)tropical moist broadleaf forest, **(b)** desert and xeric shrubland, **(c)** temperate broadleaf mixed forest, and **(d)** temperate grassland, savanna, and shrubland. Dots and lines represent, respectively, the empirical (ePNOF) and the calculated (cPNOF).

530 **Table 1**

Biome	Number of studies	Number of species	Number of species in the optimum pH ($S_{opt,j}$)	pH range of species occurrence	(Range of) pH optimum
(Sub)tropical Moist Broadleaf Forest	17	533	358	3 to 8.2	4.1
(Sub)tropical grassland, savanna, and shrubland	3	131	107	4.5 to 6.1	4.9
Mangrove	2	25	25	3.4 to 7.2	4.3 to 6.0
(Sub)tropical dry broadleaf forest	3	139	65	5.5 to 8.5	7
Flooded grassland and savanna	2	18	18	5.3 to 6.9	5.9 to 6.6
Desert and xeric shrubland	17	350	293	5.1 to 10.5	7.4
Mediterranean Forest, Woodland, and Shrubland	4	31	13	4.9 to 8.6	7.8

Biome	Number of studies	Number of species	Number of species in the optimum pH ($S_{opt,j}$)	pH range of species occurrence	(Range of) pH optimum
Temperate Broadleaf Mixed Forest	55	682	473	2.4 to 9.4	4.7 to 5.1
Temperate Grassland, Savanna, and Shrubland	17	422	325	2.6 to 9.1	5.1 to 5.7
Temperate Coniferous Forest	8	230	191	3.1 to 8.3	4.7 to 4.8
Montane grassland and shrubland	2	138	138	5.5 to 7	6.0 to 7.0
Boreal Forest / Taiga	4	90	77	3.2 to 7.7	5.3
Tundra and alpine	6	171	111	4 to 7.9	7.0 to 7.3

531

532

533 **Table 2**

Biome	α	β	Pseudo – R ² ^b
(Sub)Tropical Moist Broadleaf Forest	3.55 (3.51 to 3.6)	0.18 (0.14 to 0.22)	0.97
(Sub)tropical grassland, savanna, and shrubland	4.55 ^a (4.40 to 4.70)	0.16 ^a (NS)	
Mangrove	3.72 (3.67 to 3.77)	0.25 (0.20 to 0.30)	0.95
(Sub)tropical dry broadleaf forest	Model did not fit the empirical data		
Flooded grassland and savanna	5.31 (5.10 to 5.51)	0.33 (0.14 to 0.53)	0.73
Desert and xeric shrubland	6.76 (6.68 to 6.83)	0.36 (0.28 to 0.36)	0.94
Mediterranean Forest, Woodland, and Shrubland	6.64 (6.21 to 7.08)	1.18 (0.54 to 1.83)	0.42
Temperate Broadleaf Mixed Forest	3.57 (3.53 to 3.61)	0.36 (0.32 to 0.40)	0.98
Temperate Grassland, Savanna, and Shrubland	4.42 (4.37 to 4.47)	0.26 (0.22 to 0.31)	0.95
Temperate Coniferous Forest	3.33 (3.17 to 3.50)	0.28 (0.11 to 0.44)	0.65
Montane grassland and shrubland	5.92 ^a (NS)	0.01 ^a (NS)	

Boreal Forest / Taiga	4.21 (4.09 to 4.32)	0.69 (0.55 to 0.84)	0.89
Tundra and alpine	4.76 (4.62 to 4.90)	0.47 (0.33 to 0.61)	0.86

^a One (or both) logistic coefficients are non-significant at a 95% confidence level

^b $Pseudo-R^2 = 1 - \frac{SS_{residual}}{SS_{corrected}}$, as defined by Schabenberger and Pierce (2001)